International Journal of Bifurcation and Chaos, Vol. 17, No. 10 (2007) 3409–3414

NEOCORTEX'S SMALL WORLD OF FRACTAL COUPLING

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Received October 18, 2005; Revised March 15, 2006

Biological neocortical neurons are arranged in a columnar clustered architecture. Using a mathematical model in which the clustering properties can be monitored by means of a connectivity probability function, we investigate the information propagation in the associated networks, by means of simulations and a semi-analytical approach. Our analysis demonstrates that for systems with n-nearest neighbor coupling, the information propagation increases linearly in the neighbor order n. For fractal coupling, shown to give rise to small-world network characteristics, in contrast, an enhanced dependence is found, that, in our model of the neocortex, quickly saturates at a high level, indicating the superiority of this network type.

Keywords: Fractally coupled networks; topological properties.

1. Introduction

Complex relationships can often be abstracted into a network of nodes, where the interactions between the nodes are represented as edges. A recent observation made in this context is that many real-world systems show a small-world structure [Albert & Barabasi, 2002]. Watts and Strogatz [1998] introduced a paradigm that, by rewiring the links between the nodes, leads from n-nearest neighbor coupled networks via small-world networks to randomly coupled networks (see also [Newman & Watts, 1999]). Two parameters are generally used in order to describe this transition. The mean path length L (defined as the mean of the shortest path between all pairs of nodes) specifies salient global features of the network. In contrast, the clustering coefficient C (defined as the average number of connections between the neighbors of a node, divided by the number of edges of a globally coupled neighborhood) is an important local characterization of the network. Imagine a (pure) n-nearest neighbor coupled network ($n \gg 1$), which implies large L and C. Rewiring randomly a small portion of the links leaves the local network structure almost unchanged (preserving the large value of C), reduces, however, greatly the mean path length L, by means of shortcuts. The resulting networks are called small-world networks. A further increase of the rewiring probability leads to a randomly coupled network, where L and C are both small [Watts & Strogatz, 1998].

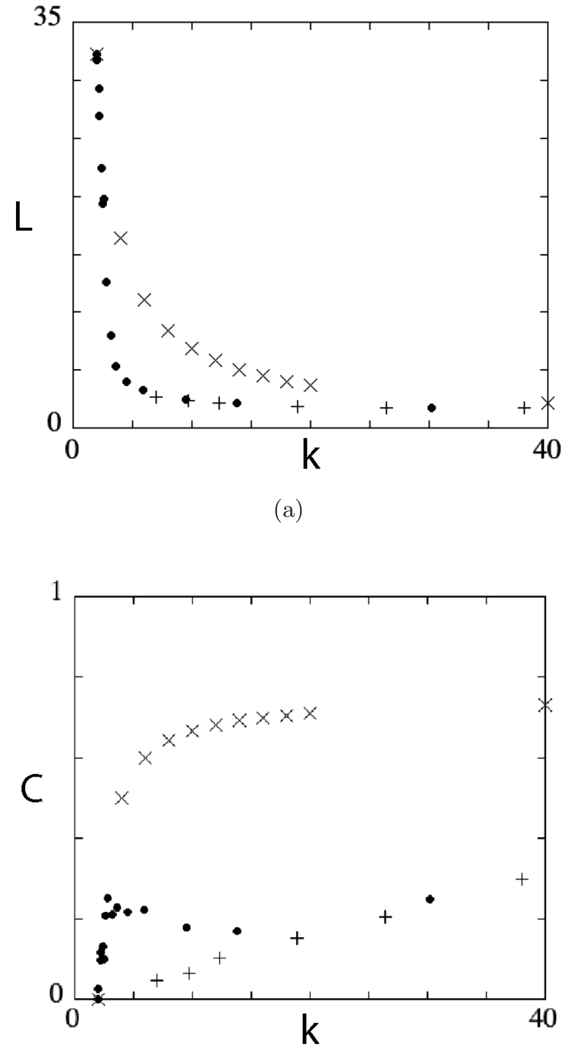
The graph degree k, i.e. the average across the graph of the number of edges emanating from a node, is a simple and convenient macroscopic parameter to go from networks of low to high connectivity. We will use the characteristics L and C to specify the properties of fractally coupled networks (FCNs). The latter network type was introduced by Raghavachari and Glazier [1995], inspired by fractal structures of dendritic trees. If the probability for the existence of a connection between the locations r_i and r_j is given by

$$p_{i,j} \propto |r_i - r_j|^{-\alpha}, \tag{1}$$

the number of connections in a d-dimensional sphere of radius R scales with $R^{d-\alpha}$, where α is a semi-positive real number, hence the term fractal.

The exponent α determines the graph degree. Increasing α from zero to infinity, the network changes its characteristic from a globally coupled network, via fractally coupled networks, to next-neighbor coupled networks. Interestingly, fractal connection distributions were recently experimentally found in the visual cortex $V1$ of ferrets. This neocortical neuronal network is organized in a columnar structure, where the neurons within a column code for the same feature in the visual field [Bear *et al.*, 1996]. Roerig and coworkers [Roerig & Chen, 2002] determined the dependence of the number of connections to a central neuron on the distance, and found a long-tail histogram that can nicely fit a power-law (not shown). Since the target neurons are located in orientation columns that have a well-defined diameter, it is plausible to assume that the distance distribution between neurons is well-represented by the distance distribution between a neuron and its synaptic inputs.

In our work, we will model this columnar network structure, extract its topological properties, and investigate the information transfer between the columns. By using Eq. (1), we will artificially generate the corresponding topology and superimpose it with the temporal dynamics of a coupled map lattice, so as to take account of the temporal aspects. The importance of coupled map lattices in capturing essential features of extended systems in biological sciences was already pointed out by Kaneko [1994]. Our numerical simulations will reveal that in fractally coupled clusters, information propagation is enhanced, if compared to n-nearest neighbor coupled networks having an equal connection density.



(a)

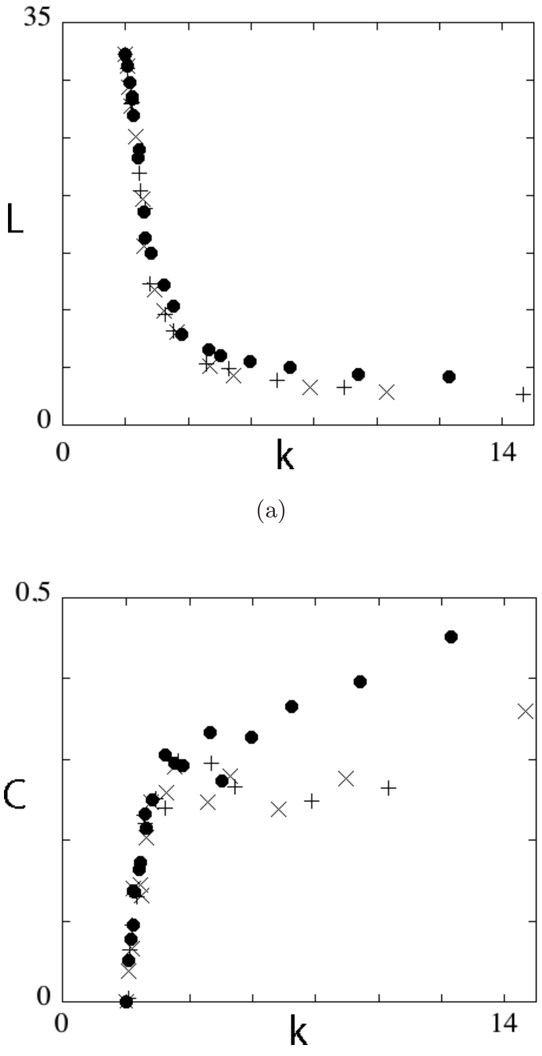
(b)

Fig. 1. (a) Mean path length L and (b) clustering coefficient C versus the graph degree k for $n = k$-nearest neighbor coupled networks (crosses), FCNs (circles), and randomly coupled networks (plusses). Network size: $N = 128$. Shown results are from individual trials. For all trials, they were close to the ensemble averages.

2. Topological Properties of Fractally Coupled Networks

We first concentrate on the topological aspects of FCNs. We will analyze how their mean path length L and clustering coefficient C depend on graph degree, and compare this with randomly coupled and n-nearest neighbor coupled networks of the same node degree. We use reciprocal connectivity and periodic boundary conditions.

The degree of a node is defined as the number k of links that either point to the node, or origin at the node. The network is represented as a linear chain with unitary distance between neighboring elements. In order to obtain a FCN, we select one node and with probability $1/R^{\alpha}$ connect it to any other node, where R denotes the distance between the nodes. The steady state distribution for $\alpha = 0$ ($k = N - 1$) is a randomly/globally coupled network, whereas for $\alpha \to \infty$ ($k = 2$), the system reduces to a first-nearest neighbor network [Raghavachari & Glazier, 1995]. Figure 1 displays the parameters L and C for purely n-nearest neighbor, fractally coupled, and random-coupled networks. Interestingly, the values $L \simeq 2.5$ and $C \simeq 0.13$, obtained for $N = 282$ in the whole relevant range, are quite close to those obtained for the neuronal network of the biological example



(a)

(b)

Fig. 2. (a) Mean path length L, and (b) clustering coefficient C, versus the graph degree k for columnar FCNs. Circles: $\{cs = 8,\ nc = 1\}$, plusses: $\{cs = 16,\ nc = 1\}$, crosses: $\{cs = 8,\ nc = 2\}$. Network size: $N = 128$. Shown results are from individual trials. For all trials, they were close to the ensemble averages.

C. elegans ($L = 2.65$, $C = 0.28$, for $N = 282$ [Watts & Strogatz, 1998]).

The FCN is characterized by a fast decay of L, which is due to the abundance of long-range interactions already at high values of the exponent α (corresponding to low values of k). Therefore, L of the fractally coupled network rapidly approaches the values of the randomly coupled network, which for $k \leq 6$ is a decoupled network. In contrast, the clustering coefficient C of the fractally coupled network increases strongly because of the increased probability of short-range connections. The plateau region around $k \leq 20$ following the increase, is caused by the large number of unconnected neighbors due to the increased probability of shortcuts. In the region $3 \leq k \leq 10$, the fractally coupled network's mean path length L is comparable to that of the randomly coupled network, whereas its clustering coefficient C largely exceeds that of the randomly coupled network. This shows that FCNs are small-world networks, and therefore can be expected to provide efficient information propagation [Latora & Marchiori, 2001].

For a more biologically detailed model of the visual cortex $V1$, we divided the original chain comprising N elements into N/cs columnar clusters of size cs. The connections from a given column were restricted to its nc-nearest neighbor columns. Within this range, the distribution of connections follows the power-law Eq. (1). This was implemented by putting all neurons on a line, partitioning the line into chunks of cs neurons. Above each neuron, the two-sided (power-law) connectivity probability function is drawn, truncated where the nc-nearest columnar clusters end, and the connections are chosen accordingly.

To estimate the parameters L and C of this system, we used a network of size $N = 128$. For a first simulation, a columnar cluster size of $cs = 8$ and a coupling range of $nc = 1$ was chosen. As is shown in Fig. 2, in the interval $3 \leq k \leq 10$, a dependence of L and C characteristic for small-world networks is observed. When we changed $cs = 8$ to $cs = 16$, and $nc = 1$ to $nc = 2$, we noticed no substantial change, indicating the stability of the observation. The large value of C is maintained across a range larger than that covered by the column: The larger the column size, or the larger the number of coupled nearest-neighbor columns, the more pronounced it is.

3. Site Dynamics

To demonstrate the relevance of the results of the previous paragraph for the dynamical environment, we need to detail the temporal evolution of our model. As the neural network site maps, we chose chaotic logistic oscillators $f(x(n)) = 1 - ax^2(n)$. Their interaction is modeled by diffusive coupling

$$x_i(t+1) = (1-\varepsilon)f(x_i(t)) + \frac{\varepsilon}{A_i}\sum_{j\in\text{conn}} f(x_j(t)), \tag{2}$$

where t denotes time, A_i the number of connections to/from the ith site, and j runs over all sites that are connected to site i. The information velocity along the chain will be estimated by means of the maximal velocity of the propagation of perturbations through the network [Cencini & Torcini, 2001; Giacomelli *et al.*, 2000]: A small perturbation is applied to the oscillators of a columnar cluster, and the information propagation is followed using the difference to a replica system without perturbation. The information propagation velocity v^* can directly be measured from the perturbation at the leftmost and the rightmost oscillator. For $\alpha \to \infty$, the information propagation can be understood as the result of two independent contributions: the chaotic instability of the map leads to an average exponential growth of the initial perturbation d_0, whereas the diffusive coupling results in a Gaussian spreading. The combined effects are then given by the equation [Giacomelli *et al.*, 2000]

$$|\delta x_i(t)| \approx \frac{d_0}{\sqrt{4\pi D t}}\, e^{(\lambda t - \frac{i^2}{4Dt})}, \tag{3}$$

where t represents time, i labels the site, D denotes the diffusion coefficient, λ is the Lyapunov exponent of the site map, and d_0 is the perturbation strength. The evolution of an initially localized, infinitesimal perturbation can be described by the convective Lyapunov exponent [Giacomelli *et al.*, 2000]. It expresses the growth rate of a disturbance when measured from a frame moving with velocity v. For spatially symmetric chaotic systems, the convective Lyapunov exponent Λ is symmetric with respect to $v = 0$, with the maximum at the origin. At the critical value of the velocity $v = v^*$, the convective Lyapunov exponent vanishes, as perturbations that travel faster than v^* are exponentially damped. The velocity of the traveling wave front is determined at the borderline of damped and undamped perturbations, which is given by $\Lambda(v^*) = 0$. This yields for the critical velocity

$$v^* = 2\sqrt{D\lambda}. \tag{4}$$

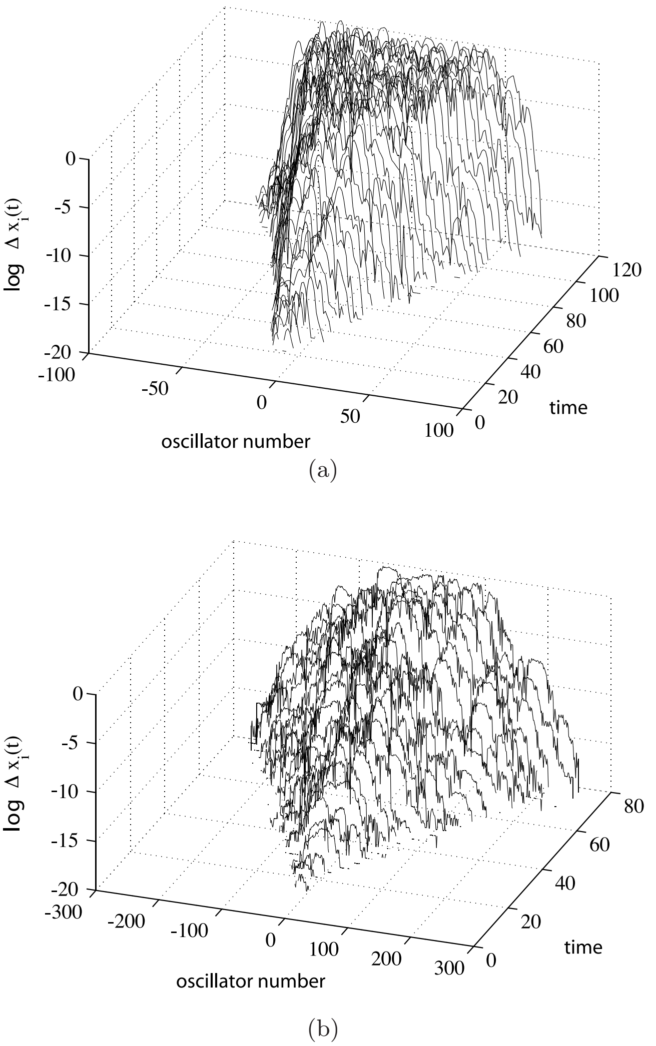


Fig. 3. Propagation of perturbations in fractally coupled clustered networks, for (a) $\alpha = 10$ (corresponding to n-nearest-neighbor coupling ($k \sim 1$)) and (b) $\alpha = 0.6$ [$k \sim (9/2)$]. Further parameters: $N = 512$, $cs = 8$, $nc = 1$, $\varepsilon = 0.8$, perturbation strength $d_0 = 10^{-8}$, site map parameter: $a = 2$.

4. Simulation Results

To track perturbation propagation, we use the difference between the original network $x_i(t)$ and a replica system $x_i'(t)$, $\Delta x_i(t) = |x_i(t) - x_i'(t)|$. A whole columnar cluster (oscillator indices $i = -7$ to 0) was perturbed by adding a perturbation of size 10^{-8} to the actual value of each cluster element. In the semi-logarithmic plot of Fig. 3, typical perturbation evolutions are shown, based on a chain of $N = 512$ oscillators. As before, for panel (A) $\alpha = 10$ was chosen, for panel (B) $\alpha = 0.6$. The perturbation velocity was estimated following the suggestion of [Cencini & Torcini, 2001]. For the two values of α shown in Fig. 3, we obtain a more than five-fold increased speed for the FCN. Whereas the width of the wavefront is related to the maximal coupling radius, its ruggedness is related to the degree of incomplete coupling (see Fig. 3). Part of the increased information propagation observed for fractal coupling is due to the larger number of connections. For Fig. 4, which shows a comparison between the propagation speed in FCNs versus n-nearest neighbor coupled networks, we therefore used networks with the same number

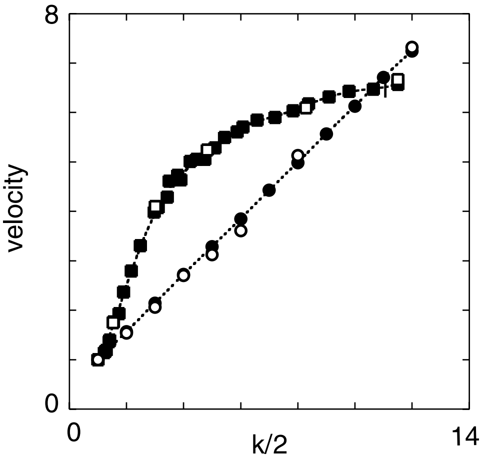


Fig. 4. Information velocity versus connectivity for different chaotic maps. Velocities are scaled by the first-nearest neighbor coupling velocity. Circles: nearest neighbor networks, Squares: FCNs (site map parameter: $a = 2$). Open symbols: simulations, Filled symbols: semi-analytical results. Broken lines are guidelines to the eye. The observed saturation is an effect by the columnar structure of the network. The results for $a = 1.9$, and the symmetric fully developed tent map closely follows the displayed results.

of connections. For n-nearest neighbor coupled networks, a linear increase of the velocity on the connectivity was observed. This increase, however, is vastly outperformed by the enhanced information propagation in the fractally coupled columnar clusters.

5. Semi-Analytical Approach

In view of Eq. (4), the origin of the increased information transfer is a joint effect in the diffusion coefficient D and the Lyapunov exponent λ. We have therefore studied the dependence of the diffusion coefficient on the network configuration, using a Markov chain model. From the connectivity matrix and the interaction strength $\varepsilon = 0.8$, the transition matrix P of the Markov process can easily be derived. Care must be taken to scale P so that the entries of each row sum up to unity. Two absorbing states are put at the ends of the chain. The time τ it takes for a perturbation to diffuse from the center of the chain to either end, can be calculated via the fundamental matrix of P [Kemeny & Snell, 1976]. Denoting this distance by Δs, the diffusion coefficient can be evaluated as $D = (\Delta s^2/2\tau) \approx (N^2/8\tau)$. For first-nearest neighbor coupling, the diffusion coefficient $D_0 = \varepsilon/2$ and the critical velocity $v_0^* \approx 0.72$ are well known [Cencini & Torcini, 2001]. Allowing for a small variation of the convective Lyapunov exponent only, the speed of the wave front can be approximated by $v(\mathrm{co})^* = v_0^* \sqrt{(D(\mathrm{co})/D_0)}$ [see Eq. (4)], where co indicates the dependence on the network architecture.

The results of this calculation for a network with an increasing number of nearest-neighbors and for the FCN are included in Fig. 4 (full symbols). In both cases, a good agreement between the calculated and the simulated velocities is obtained. Since the velocity enhancement is due to the increase of the diffusion coefficient, the superiority of the fractal network, compared to other networks with decaying connection probabilities, is based on the particular structure of its transition matrix. Fast diffusion is achieved if sites far apart are connected (nonzero matrix element far off the diagonal). Moreover, the probability for such transitions must be high. This decreases the probability for short-distance jumps, as the transition probabilities emanating from a site sum up to unity. These two conditions force the probability density to decay quickly in the short-range, and to have a long tail in the long-range. The power-law of fractal coupling optimally satisfies these requirements, if compared to exponential coupling $p_{i,j} = \exp(-\mu \mid r_i - r_j \mid -1)$, Gaussian coupling $p_{ij} = \exp(-\gamma(\mid r_i - r_j \mid -1)^2)$, and n-nearest neighbor coupling. For a realistic simulation of the columnar neocortical networks, the intro-columnar connectivity needs to exceed the intercolumnar connectivity. When α is varied from 0, 0.2, 0.6, 1, 2, 5 to 10, the mean connections per site decreases from 11.5, 8.29, 4.81, 2.99, 1.57, 1.02 to 1. The neocortical situation is thus met for $\alpha > 0.8$, where $k/2 < 4$ holds. As can be seen in Fig. 4, in this range the velocity enhancement is maximal.

6. Summary

We explored the properties of a one-dimensional model of the neocortical network $V1$, where the probability p of a connection follows a power-law $p \approx R^{-\alpha}$, R denoting the internode distance. If the exponent α changes from 0 to ∞, this transforms the system from a globally coupled into a first-nearest neighbor coupled network. For intermediate values of α, our analysis revealed that FCNs can be classified as small-world networks, where the classification relies on the values of the mean path length L and the clustering coefficient C.

On a clustered network structure mimicking $V1$, we introduced dynamical behavior by representing the neurons as chaotic oscillators. In these networks, we studied the information propagation by simulations and semi-analytically. We found a considerable increase in speed for fractal coupling, over all other compared network types. In the semi-analytical approach, the propagation velocity is determined in terms of the Lyapunov exponent of the oscillators and the diffusion coefficient of the chain [Eq. (4)]. Using a Markov process formulation, which takes into account the connection scheme as well as their coupling strength, we could easily evaluate the diffusion coefficient. The obtained results coincide with the numerical simulations to great accuracy. The Markov process explicitly shows that fast information propagation is mediated by means of long-range connections. In FCNs, these are located in the long tail of the power-law probability distribution. In order to increase the probability of the long-range connections, the number of short-range connections needs to be reduced. If we compare the dynamic simulations with the network analysis, we find that the propagation enhancement goes in parallel with a decrease in the mean path length. In contrast, the increased clustering coefficient cannot be seen as an origin of the velocity enhancement. Rather, it is required in order to keep the network connected.

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